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Acoustic allometry and vocal learning in mammals

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Abstract

Acoustic allometry is the study of how animal vocalisations reflect their body size. A key aim of this research is to identify outliers to acoustic allometry principles and pinpoint the evolutionary origins of such outliers. A parallel strand of research investigates species capable of *vocal learning*, the experience-driven ability to produce novel vocal signals through imitation or modification of existing vocalisations. Modification of vocalizations is a common feature found when studying both acoustic allometry and vocal learning. Yet, these two fields have only been investigated separately to date. Here, we review and connect acoustic allometry and vocal learning across mammalian clades, combining perspectives from bioacoustics, anatomy and evolutionary biology. Based on this, we hypothesize that, as a precursor to vocal learning, some species might have evolved the capacity for volitional vocal modulation via sexual selection for ‘dishonest’ signalling. We provide preliminary support for our hypothesis by showing significant associations between allometric deviation and vocal learning in a dataset of 164 mammals. Our work offers a testable framework for future empirical research linking allometric principles with the evolution of vocal learning.

Keywords: phenotypic plasticity; evolution of communication; evolution of speech; allometric scaling; vocal production learning

Constraining and modulating vocal signals

Body size affects multiple aspects of animal behaviour, often predicting the outcome of agonistic or mating interactions [1]. Sexual selection over vocal communication systems has led to cases where the body size of the caller is accurately reflected in the acoustic features of its vocalisations, i.e. honest signalling [2, 3]. This principle also applies to species that have evolved special anatomical adaptations to modify their vocalisations [4]. Often, these anatomical modifications appear to be driven by ‘dishonest’ signalling, where adaptations can create an exaggerated impression of body size. However, such physical modifications ultimately bound the acoustic features of vocalisations similarly for all individuals within a species (i.e. runaway selection is constrained [5, 6]). Therefore, these vocalisations are still considered honest signals within the species, only shifted from what is expected when compared to other, similarly-sized species (as in red deer [2] and koalas [7]). The investigation of acoustic allometry mainly involves two categories of acoustic features defined following the source-filter theory of voice production: the fundamental frequency (f_0) and formant frequencies [8]. f_0 corresponds to the rate of vibration of vocal folds located in the mammalian larynx, i.e. the sound source, while formant frequencies are specific resonances reflecting the geometry of the mammalian vocal tract, i.e. the filter. Across mammal species, f_0 provides allometric cues to body size [9-11], but these are far less reliable than formant frequencies [4], likely because laryngeal anatomy is less constrained than vocal tract anatomy by surrounding skeletal structures [3].

Vocal production learning (VPL) can be defined as the experience-driven ability, rare among mammals, to modify existing vocalisations, to produce novel sounds or to imitate sounds that do not belong to an individual’s vocal repertoire [12, 13] (for usage learning, see [14]). VPL inherently involves modulation of acoustic features related to the source, filter or both. Yet, different species have varying degrees of control over the anatomical components involved in phonation. For instance, despite a generally assumed lack of vocal control [15], some non-human primates might have limited sound production plasticity [15-17], including for non-voiced sounds [18]. While the presence of VPL in non-human primates is debated [19-22], strong evidence for VPL has been found to date in humans and four other mammalian clades: non-otariid Pinnipedia, Elephantidae, Chiroptera, and Cetacea [23-26]. These four taxa (henceforth VPL clades) appear particularly apt to study the evolution of VPL in the context of sexual selection. Indeed: could sexual selection push an animal to volitionally modulate its sound production, thus rendering the acoustic allometry principle unreliable [27]? Here we formalize this question and provide a framework (Figure 1) for future research investigating a potential evolutionary trade-off between overall anatomical constraints (acoustic allometry) and VPL (seen here as an allometry-cheating strategy).

Linking sexual selection on body size and vocal production learning

Figure 1 provides a stepwise framework explaining how selection for dishonest signalling could pave the way to VPL. This framework is inspired by recent work suggesting that human VPL capacities, also involved in speech, originate from sexually selected voice modulation [27]. To develop our hypothesis, we focus on the first formant frequency (hereafter F_1) to investigate the potential relationship among acoustic allometry, VPL, and sexual selection. There are three main reasons for this choice. First, the physics underlying sound production outlines an intuitive relationship: the longer a vocal tract is, the lower the F_1 it produces [28]. Due to the same underlying physics connecting single formant values and formant spacing

(the latter being more commonly used in acoustic allometry studies, e.g. [29]), we rely on information redundancy between these features and prefer F_1 for ease of illustration and communication. Second, acoustic allometry studies have typically shown more conclusive evidence for body size scaling with formants, rather than f_o [4]. Third, using F_1 reflects the formant modulation often seen in the vocalisations of VPL mammalian species (henceforth VPLs) produced while imitating vocal patterns [30, 31]. Yet, our reasoning equally applies to other features used when investigating acoustic allometry in mammals, e.g. individual formants, formant spacing or f_o [7, 9, 32]. The underlying rationale (detailed in Figure 1's legend) is that, in some species, sexual selection may have driven allometry-cheating sound modulation as a precursor to VPL.

Figure 1. Conceptual representation of a species' repertoire, corresponding to the probability $p(F_1)$ of uttering vocal signals with a formant frequency F_1 , which can be affected mainly by anatomical constraints (a-c) or volitional vocal modulation (d). **a)** F_1 variation in a model species is distributed around a mean frequency (grey vertical line) and remains constrained by allometric principles acting on vocal tract length. This sketches the typical F_1 distribution for most mammal species identified as non-vocal learners (non-VPLs) to date (e.g. [32]). **b)** Hypothetical F_1 distributions for three different species. Whiskers correspond to the truncated tails of the distributions, showing how variation in F_1 is constrained by anatomical limits across species. **c)** Within a given species, sexual selection pressures can induce an evolutionary shift of distributional constraints due to anatomical modification of the vocal tract through dishonest signalling (corresponding in this example to body size exaggeration, i.e. elongation of the vocal tract visualized as a left-skewed F_1 distribution). This is the case, for example, in koala, red deer and saiga antelopes [7, 33, 34]. Note that dishonest signalling towards body size reduction could in principle equally apply. **d)** Under relaxed selective pressure for dishonest signalling, volitional vocal modulation (*sensu* [27]) allows active control over the F_1 distribution. While acoustic allometry rules are still inherently present, deviation from standard allometric constraints can be achieved through sound modulation, as opposed to being an acoustic by-product of anatomical adaptations (i.e. panel c). Over time, the allometry-cheating mechanism in place further increases the capacity for volitional vocal modulation and can lead to full VPL. **e)** Theoretical perspective on the evolution of VPL. Black boxes show intermediate steps in the framework we propose here. Grey boxes show existing alternative hypotheses for the evolution of VPL [35].

Stepwise acquisition of vocal modulation via dishonest signalling

Based on available empirical evidence and comparison of abstract cases in Figure 1, we propose a theoretical framework connecting VPL and acoustic allometry. Based on our multistage model (Figure 1e), we suggest that:

- (i) in most species, *selection pressure for honest signalling* is high [36, 37];
- (ii) in the context of sexual selection, *deviating from allometric scaling* between acoustics and body size may be achieved by producing dishonest signals in agonistic interactions, mate attraction and territorial advertisement contexts; *dishonest signalling* can be *evolutionarily stable* as long as it is not deployed too often within or across individuals [36, 37]; however, acoustic variation within vocalisations can occur in the process and lead to either (iii) or (iv);
- (iii) in some cases, signals would evolve together with purely *anatomical adaptations* and ultimately provide a case of honest signalling within the species through runaway selection

(Figure 1c, [5, 6]);

(iv) in other cases, signalling body size dishonestly could lead to *increased motor control of the vocal apparatus*, with volitional sound modulation throughout the species-specific vocal production range (i.e. the allometry-cheating modulation seen in Figure 1d, occurring in species where selection for dishonest signalling overpowered that for honest signalling);

(v) furthering this enhanced control, originally developed to dynamically escape allometric constraints, can be a stepping stone towards the acquisition of VPL and this control could be co-opted in other social contexts to eventually

(vi) result in full VPL.

In the framework presented here, VPL would thus constitute the end result of an emerging capacity to circumvent the limitations imposed by acoustic allometry. Once VPL has emerged, it can only be evolutionarily stable if sexual selection does not depend entirely on allometric principles. We hypothesise that in VPLs a selective shift may occur, whereby dynamic allometry-cheating is maintained via *sexual selection acting upon acoustic phenotypic plasticity* (volitional F_1 modulation anywhere across $p(F_1)$) instead of static cues to body size (whiskers delimiting $p(F_1)$).

To highlight our reasoning, we examine the relationship between acoustic allometry and vocal learning based on available data from most known cases of VPL clades (Figure 2, Tables 1-2 and [11]). Our results overall suggest a statistical association between VPL and deviation from acoustic allometry, based on a greater proportion of allometric outliers (Figure 2, minimum dominant frequency), and larger absolute deviation, in VPL clades (Table 1), observed from phylogenetically controlled acoustic allometry regressions (see Electronic Supplementary Material for details). Careful consideration of these results is required because our analysis treats all species in a VPL clade as VPLs, regardless of the number of VPLs in that clade. Nonetheless, our framework and analyses hold promising predictive potential for further research on vocal learning, as they provide a way to identify new candidate VPLs (bottom row Table 1; Supplementary Figures 2 & 3). In addition, we emphasize the hypothesized synergy between allometry-cheating strategies, sexual selection and VPL. For this, we review (Table 2) the evidence for sexual selection on vocalisations, acoustic modulation, and deviation from allometric rules in all currently known mammal VPL species.

Figure 2. Bar charts outlining the proportions of allometric outliers within VPL and non-VPL clades. Acoustic allometry is assessed through the use of dominant frequency (or peak frequency), and VPL clades are defined as clades which include multiple known VPL species (i.e. by extension, our analysis assumes VPL ability for all species that belong to a VPL clade; see Supplementary Figures 2 & 3 for additional analyses and Supplementary data, adapted from [11]). The proportion of allometric outliers is significantly greater in VPL than non-VPL clades when investigating allometry scaling based on minimum dominant frequency (Barnard's test: $Z = -5.29$, $P < 0.001$), but not maximum dominant frequency ($Z = 1.2$, $P = 0.24$).

Table 1. Comparison of the residuals from acoustic allometry regressions using Mann-Whitney U tests.

Acoustic trait	Minimum frequency	Maximum frequency
Median of residuals for VPL clades	0.79	0.37
Median of residuals for non-VPL clades	0.38	0.29
W-value	4943	3838
p-value	< 0.001	< 0.01
Five outlier species with the largest residuals among non-VPL clades (i.e. potential candidate VPLs)	<i>Trichechus inunguis</i> <i>Arctocephalus tropicalis</i> <i>Meles meles</i> <i>Eulemur coronatus</i> <i>Mus musculus</i>	<i>Cervus elaphus</i> <i>Arctocephalus philippii</i> <i>Mus musculus</i> <i>Ailuropoda melanoleuca</i> <i>Pongo pygmaeus</i>

Table 2. Clade-wise investigation of allometry scaling and VPL

Clade	Species	Sexual selection on vocalizations	Acoustic modulation	Escaping allometric rules	VPL
Pinnipedia	<i>Phoca vitulina</i> (Harbor seal)	Intra- [38] and inter-sexual [39]	Mainly formants [23, 40]	Ability to modulate acoustic features [38] that could otherwise signal their body size [41]	Yes (imitation) [23, 40]
	<i>Halichoerus grypus</i> (Grey seal)	Suggestive evidence [42] and non-vocal signalling [43]	Formants [44]	Empirical data lacking	Yes (imitation [44] and usage learning [45])
	<i>Mirounga leonina</i> (Southern elephant seal)	Intra-sexual [46]	Mostly temporal [46]	Low explained variance (10%) in the formants vs. body size regression [47]	Yes (copying call types of successfully breeding individuals) [46]
	<i>Odobenus rosmarus</i> (Walrus)	Intra- [48] and inter-sexual [48]	F0 [49] and call combination [50]	Empirical data lacking, but acoustic resonance effect of pharyngeal pouches [3] could potentially induce modified perceived size information	Yes (but contingency learning) [50]

Elephantidae		<i>Loxodonta africana</i> (African elephant)	Intra- and inter-sexual [51]	F0 and formants [52, 53]	Cues to body size [53, 54] modifiable through active shift between orally- and nasally-emitted calls [53], flexible trunk-length adjustment [55] and mobile larynx [56]	Yes (imitation [52] and adequate neural bases [24])		
		<i>Elephas maximus</i> (Asian elephant)	Intra- and inter-sexual [57]	F0 and formants [30]		Yes (imitation) [30]		
Chiroptera		<i>Phyllostomus sp.</i> (Spear-nosed bats)	Intra-sexual [58]	F0 [59]	Non-significant body mass-peak frequency relationship across species [60]	Yes [25, 59, 61]		
		<i>Saccolpteryx bilineata</i> (Greater sac-winged bat)	Intra- and inter-sexual [62]	F0 [63] and babbling [64]	Lack of F0-body size correlation [65]	Yes (tutor imitation) [25, 63]		
Cetacea	Odontoceti (Toothed whales)	<i>Tursiops truncatus</i> (Bottlenosed dolphin)	Anecdotal evidence for inter-sexual [66]	Extensive F0 [67]	Low explained variance (27%) in the minimum F0 vs. body size regression [68] and no correlation with other acoustic features (as expected given the changes in formants induced by variation in pressure at different depths [69]); no correlation with body mass and acoustic features [68]	Yes (imitation, innovation) [26, 70]		
		<i>Orcinus orca</i> (Killer whale)	Empirical data lacking	F0 [71]		Yes (imitation) [26]		
		<i>Grampus griseus</i> (Risso’s dolphin)	Empirical data lacking	F0 [72]		Yes (imitation of heterospecific whistles) [72]		
		<i>Delphinapterus leucas</i> (Beluga whale)	Anecdotal evidence [73]	F0 and formants [74]		Yes (imitation) [26, 74]		
	Mysticeti (Baleen whales)	<i>Megaptera novaeangliae</i> (Humpback whale), <i>Eubalaena sp.</i> (Right whale) and <i>Balaena mysticetus</i> (Bowhead whale)		Suggestive evidence for intra- and inter-sexual [75]		F0 and formants [76-78]	Yes (imitation, innovation) [26]	
Hominidae		<i>Homo sapiens</i> (Human)	Intra- and inter-sexual contexts [79, 80]	F0, formants, temporal [27, 81]	Weak allometric scaling between F0 and body size despite use of F0 in sexual selection; allometric scaling with formants much better than F0 although moderate (10%) explained variance in body size [82]	Yes (imitation, innovation, enhanced vocal control) [35, 83-85]		

Alternative allometry-cheating scenarios

We naturally acknowledge the fact that sexual selection on vocal features can also occur in non-VPLs. Similarly, other selective pressures may drive allometry-cheating strategies among

mammals (including VPLs and non-VPLs). Such pressures include, but are not limited to: 1) temperature and metabolic conditions, for which an interplay with body size and acoustic scaling has been identified in frogs [86] and could act similarly in mammals [87]; 2) adaptation of vocal signals to foraging and orientation purposes such as echolocation calls in bats and dolphins [88] (note however that echolocation calls can also carry a communicative value in these taxa [89, 90]); 3) anatomical adaptation related to the environment in which a species lives. For instance, sound production in odontocetes generally differs from that of other mammals: phonic lips in the nasal airway vibrate to produce echolocation clicks and whistles [91]. In this particular clade, we note only very scarce evidence for sexually-selected vocalisations (Table 2); instead, sound production for orientation or foraging purposes [88] could have driven deviations from allometric scaling. Until additional investigations on the presence and relevance of sexually selected vocalisations and the nature of allometric relationships in odontocetes are undertaken, the origin of allometry-cheating in this clade remains unknown. Similarly, evidence for acoustic allometry (or deviation from it) in grey seals is also lacking (Table 2). We stress that our framework is non-exclusive, illustrating one possible evolutionary mechanism toward the emergence of VPL, which rests on suggestive initial evidence (Figure 2 & Supplementary Figures 2 & 3; see also [27]) but remains to be tested empirically and on a large scale.

Conclusions and future work

This paper provides one evolutionary hypothesis (in addition to others, already proposed elsewhere [35]) for the acquisition of the capacity for VPL in mammals, including humans, through signal dishonesty. This implies a combination of enhanced motor control over voice modulation and selective pressures acting towards dishonest signalling. In this sense, our framework is a natural extension of what has been previously proposed for humans [27]: controlled acoustic modulation may have been a key step towards the evolution of human speech under an evolutionary sexual constraint for dishonest size signalling. In a similar way, sexually-induced pressure for sound modulation could have led to VPL in mammals, as yet another step towards the emergence of articulated speech in humans. The human and cross-species frameworks will help link the evolution of VPL in mammals with the origins of speech in humans, and shed light on whether and how selective pressures may apply on dynamic, rather than static, aspects of the voice in VPLs.

Given the variety of degrees with which acoustic signals can be modulated, we subscribe to the idea that VPL is a continuum rather than a binary property [92] and it should be studied as such [83]. To support or refute our theoretical framework, further studies should focus on investigating acoustic allometry relationships both within and across species. Doing so will help identify species escaping vocal allometry scaling, and therefore potential candidates for VPL abilities (this predictive value is illustrated in Table 1 and Supplementary Figures 2 & 3). When identifying such candidate species, future VPL research should dissect VPL into learning to modify targeted acoustic features, in line with the modular framework for vocal learning [93]. Conducting joint analyses of VPL and allometry, we predict quantitative differences among species displaying (1) allometric scaling of acoustic features and no VPL, (2) both allometry and VPL, (3) VPL but no allometry and (4) neither VPL nor allometry. In most cases, we expect our predicted relationships to hold stronger for F_1 or formant spacing, rather than f_0 . Such analyses can be undertaken once classification of mammals into a comprehensive VPL continuum [94] becomes available, and will require additional data to be

collected for the many mammal species for which neither allometry nor VPL has been probed [83].

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